Title

Influence of farmland abandonment on the species composition of wetland ground beetles in Kushiro, Japan

Author names and affiliations

Satoshi Yamanaka[a, b], Takumi Akasaka[c], Yuki Yabuhara[b, d], Futoshi Nakamura[b]

[a] Hokkaido Research Center, Forestry and Forest Products Research Institute, Hitsujigaoka 7, Sapporo, 062-8516, Japan

[b] Department of Forest Science, Graduate School of Agriculture, Hokkaido University, Kitaku Kita9 Nishi9, Sapporo, 060-8589, Japan

[c] Laboratory of Conservation Ecology, Obihiro University of Agriculture and Veterinary Medicine, Nishi 2-sen 11, Inadacho, Obihiro 080-8555, Japan

[d] Institute of Technology and Science, The University of Tokushima, 2-1 Minami-Josanjima, Tokushima 770-8586, Japan

Corresponding author

Satoshi Yamanaka

yamanakas@ffpri.affrc.go.jp

Tel: +81-11-590-5543

Fax: +81-11-851-4167

Abstract (233 words)

Depopulation trends in many developed regions are resulting in an increase in areas of abandoned farmland, which could provide an alternative habitat for species endangered by past conversion of wetlands for agriculture. Additionally, various spatial and temporal factors (landscape structure, local habitat quality, and abandonment age) could influence species composition in abandoned farmland. In this study, we explored the spatio-temporal effects of land abandonment on the species composition of wetland ground beetles (Coleoptera: Carabidae) to examine whether abandoned farmland can contribute to conserve wetland species' habitats. We first compared ground beetle assemblages among four land uses (grassland, wetland, and newly and previously abandoned farmland) in the Kushiro region, eastern Hokkaido, Japan. We then examined the factors influencing differences in wetland species composition between abandoned farmland and wetland. We found that the composition of wetland species in abandoned farmland was more similar to that of wetland than that of grassland. Our results also showed that soil moisture in abandoned farmland was positively related to the land abandonment age and that differences in wetland species composition between abandoned farmland and wetland were negatively related to both soil moisture and surrounding wetland area. Our findings suggest that abandoned farmland can serve as an alternative habitat for wetland ground beetles. Maintaining a high level of soil moisture in abandoned farmland and conserving the surrounding wetland could be an effective strategy for restoring natural habitats for these species.

Keywords (4-6 keywords)

Agricultural landscape; Biodiversity; Carabid; Fen; Passive restoration; Re-wilding

1. Introduction

Many developed countries are undergoing a period of transition from over-population to under-population (United Nations, 2016), and this social change has led to drastic alterations in arable land use, whereby decreasing population density is accelerating farmland abandonment (Benayas et al., 2007). Abandoned farmland can provide an alternative habitat for wildlife that has experienced range contractions due to the past expansion of arable land (Navarro and Pereira, 2015). For example, several studies suggest that abandoned farmland has contributed to the range expansion of forest-dwelling birds or large mammals in Europe (Boitani and Linnell, 2015; Sirami et al., 2008). Overall, releasing land for the natural recovery of vegetation is less costly than active restoration of degraded habitats (e.g., Barral et al., 2015; Morrison and Lindell, 2011). In addition, the conflict between conservation and development may be smaller for abandoned farmland than for other land uses. Therefore, the natural recovery of vegetation in abandoned farmland may provide a practical option for restoring wildlife habitats.

The first step toward effective restoration of abandoned farmland is to identify the factors regulating habitat conditions for target species (Sandom et al., 2013). As characterized by the vegetation or soil conditions, local habitat quality is expected to act as a primary environmental filter influencing the successful colonization of abandoned farmland (e.g., Brambilla et al., 2010), but it could also change with vegetation succession (Shoo et al., 2016). While, with regard to the dispersal ability of species and colonization processes (e.g. Hanski, 1999), the landscape structure, such as the amount of surrounding source habitat or the distance between the abandoned farmland and the source habitat, may determine the immigration potential of organisms into abandoned farmland. The importance of landscape structure can vary according to the dispersal capability of the target species (e.g., Fensham et al., 2016), and both landscape structure and dispersal capacity affect the time required for successful colonization (i.e., colonization credit; Piqueray et al., 2011). Although many studies have separately explored the effects of spatial (amount of and distance from the source habitat) and temporal (change in habitat quality) factors, few studies to date have comprehensively addressed spatio-temporal effects (Fensham et al., 2016). Although successful restoration requires colonization of individual species at the beginning stage, and also population persistence in a long time frame, in this study, we focus on the effect of these environments on the colonization of abandoned farmland by various species.

Wetland ecosystems are among ecosystems most threatened by cultivation and urbanization activities (Fujita et al., 2009; Gardner et al., 2015). Indeed, the global loss of wetland continues even today (Talberth and Gray, 2012), and the conservation and restoration of wetland habitats are of high priority because many specialist species inhabit wetland environments and most of these species are threatened (Ramsar Convention Secretariat, 2013; Zedler and Kercher, 2005). Farmland abandonment often occurs in land with low productive potential or poor drainage (high soil water potential). In addition, Kusumoto et al. (2005) demonstrated that wetland plant species can regenerate in abandoned farmland with high soil water potential. Therefore, the utilization of abandoned farmland with poor drainage conditions may be a practical option for restoring wetland ecosystems.

In the present study, we explored the spatio-temporal effects of land abandonment on the species composition of wetland ground beetles (Coleoptera: Carabidae) to examine whether abandoned farmland can contribute to wetland species conservation. We investigated 1) how the species composition of ground beetles is influenced by farmland abandonment and 2) the environmental factors that are involved.

Ground beetles were selected for the study because they comprise diverse taxa with wide distributions (e.g., Koivula, 2011), are sensitive to environmental changes and have been used as a biological indicator in various landscapes (e.g., Rainio and Niemelä, 2003).

2. Materials and methods

2.1. Study area

The study was conducted in the Kushiro region, Hokkaido, northern Japan (Fig. 1). The annual mean temperature and precipitation in the area are 6.3 °C (ranging from 5.0 to 7.7 °C) and 1057.0 mm (from 704.5 to 1577.0 mm), respectively (data from 1980 to 2015, provided by Kushiro Climatological Observatory, located within the study area). The Kushiro Wetland, the largest peat wetland in Japan, covers 19,357 ha of this region, and more than 80% of the wetland consists of fens dominated by reed, sedge, and shrubs. Since the 19th century, the Kushiro Wetland has been converted to urban land use and grassland, and 30% of the wetland was lost during the last five decades (from 28,135 ha in 1947 to 19,357 ha in the 2000s; Ministry of the Environment, 2015). However, in the 21st century, the population of the Kushiro sub-prefecture has been declining, and the abandoned farmland has been increasing (from 758 ha in 2000 to 1,691 ha in 2015; Policy Department of Hokkaido Prefecture, 2015).

For this study, we selected 37 survey sites belonging to four land uses in the Kushiro region (Fig. 1): 14 newly abandoned farmland (abandoned after the 1990s), 11 previously abandoned farmland (abandoned before the 1980s), 6 grassland (with mowed twice per year), and 6 remnant wetland (fen) sites. All survey sites in abandoned farmland areas had been wetland areas in the 1920s and were converted to grassland areas and later abandoned. The survey sites in grassland and wetland areas were selected as a reference for land use in arable land and pristine vegetation, respectively. All the survey sites were located more than 500 m apart from each other. Because no accurate data for abandonment age was available, we estimated the age of abandonment by interviewing land owners or neighbors around each survey site, and we classed the duration of abandonment into two categories: after the 1990s and before the 1980s. The dominant plant species were *Phalaris arundinacea* in both newly and previously abandoned farmland sites, *Phleum pratense* in the grassland sites, and *Phragmites australis* and *Calamagrostis langsdorffii* in the remnant wetland sites.

2.2. Ground beetle sampling

To examine the species composition of ground beetles at each survey site, we collected ground beetles using pitfall traps in two periods: early summer (June 19 to July 24) and autumn (August 27 to September 12) 2014. At each survey site, we set 16 pitfall traps placed in a grid of 2 x 8 traps for 2 weeks per period, with each trap located more than 5 m away from any other trap. Then, the grid was placed at a minimum distance of 10 m from the edge of each field. The traps were 95 mm in diameter and 124 mm in depth and contained approximately 50 ml propylene glycol as a preservative. We placed a square veneer plate (120 mm x 120 mm) above each trap to block the accumulation of rainwater. In wetland, we placed the traps on the ground, avoiding puddles, and made four or five small holes at 4 cm below the top of a trap to prevent the overflow of rainwater. The beetles were identified to the species level and categorized into three groups according to the Working Group for Biological Indicator Ground Beetles Database, Japan (2015) and Ueno et al. (1985): wetland species, open-land species, and others (including forest or generalist species). Because the “others” group contained few species and was low in abundance (12 species and 852 individuals, 5.5%

of the total abundance), we only used samples of wetland and open-land species in the subsequent analysis. All samples at each survey site were pooled for analysis. For the two survey periods, the average number of undisturbed traps was 31.5, so we normalized the ground beetle abundance based on the number of undisturbed traps at each site and used those abundance data in the analysis.

2.3. Habitat quality and landscape structure

To examine the effect of habitat quality on species composition, we surveyed vegetation density and soil moisture at each survey site in June and August of 2014. At each site, we established 16 survey points, each of which was located near a pitfall trap. We first placed a metal rod vertically at the survey point, and recorded the presence of vegetation touching the rod at 50 cm intervals (0-50 cm, 51-100 cm, 101-150 cm, and 151-200 cm). We summed all the presence/absence data of plant species for each survey point (ranging from 0 to 4) and then averaged the data for the 16 survey points for each survey site. At all 16 survey points at each site, soil moisture was measured at a depth of 15 cm using a soil moisture meter (HydroSense, Campbell Scientific, Inc., Logan, USA). The values of vegetation density and soil moisture measured in June and August were averaged for each survey site.

To examine the effect of landscape structure on the species composition of ground beetles, we made a vector map of the vegetation data, including abandoned farmland, from the latest digital vegetation map (scale of 1: 25,000; Ministry of Environment of Japan, 2004). We confirmed the locations of abandoned farmland through the interviews with farmers or local officers and through our visual observations. We calculated the patch area of abandoned farmland as an indicator of habitat quality (e.g., MacArthur and Wilson, 1967), the amount of wetland area within a

500-m buffer around the survey sites and the nearest distance between abandoned farmland and wetland, a variable that affected the colonization of abandoned farmland by wetland species from the source habitat (e.g., MacArthur and Wilson, 1967; Quesnelle et al., 2015). The size of the buffer size was chosen based on previous studies (e.g. Woodcock et al., 2010). This work was conducted using Quantum GIS version 2.8.2 (QGIS Development Team, 2015).

2.4. Statistical analysis

To assess how species composition is altered by farmland abandonment and what environmental factors influence the species composition of wetland ground beetles in abandoned farmland, we analyzed the data in two steps. First, we assessed whether there were significant differences in species composition among land uses. This analysis was performed using non-metric multidimensional scaling (NMDS) and Analysis of Similarity (ANOSIM) tests. Second, we calculated the dissimilarity index of species composition between abandoned farmland and wetland and assessed which environmental factors affected the dissimilarity index. This analysis was performed using structural equation modeling (SEM).

2.4.1. Species composition in different land uses

To examine the pattern and similarity of species composition among the four land uses, we ordinated each survey site using NMDS of two data sets in a species-abundance matrix: (1) abundance of wetland and open-land species and (2) abundance of only wetland species. The NMDS ordination was performed using Bray-Curtis dissimilarity. To alleviate the effect of rare species on the results, each data set was log transformed (log(x+1)). We described the distribution pattern of each wetland species, and we also used ANOSIM with Bray-Curtis dissimilarity to evaluate differences in species composition among the four land uses. NMDS was conducted using R ver. 3.1.2 (R development core team, 2015) and vegan package ver. 2.3-0 (Oksanen *et al.*, 2015); ANOSIM was conducted using PAST ver. 3.08 (Hammer et al., 2001).

2.4.2. Impact of environmental variables on the species composition in abandoned farmland

We applied SEM to clarify the factors that influence species composition in abandoned farmland. First, we calculated the dissimilarity index of species composition for wetland species between abandoned farmland sites (including newly and previously abandoned farmland sites) and each of six remnant wetland sites using Bray-Curtis dissimilarity (i.e., log-transformed species abundance data of wetland species), whereby a lower dissimilarity index value indicates that the composition of wetland species in an abandoned farmland site is more similar to that of a remnant wetland site. In this study, we present the mean dissimilarity index value of each abandoned farmland site.

Second, we built a full model using the dissimilarity index of each abandoned farmland site as the response variable. As explanatory variables, we used the parameters vegetation density, soil moisture, patch area of abandoned farmland, amount of remnant wetland area within a 500 m buffer, the nearest distance between abandoned farmland and wetland, and abandonment age (Fig. 4a). Abandonment age was used as a categorical variable (new, 0; previous, 1). All explanatory variables except abandonment age were log transformed, and we assumed both direct and indirect effects of abandonment age on the dissimilarity index. A direct effect indicates increasing opportunity for species immigration with time, whereas an indirect effect represents changes in habitat quality with time (vegetation density and soil moisture; Fig. 4a).

Finally, we selected the best-fitting model using stepwise specification search algorithms based on chi-square, the RMSEA (root mean square error of approximation), and the AGFI (adjusted goodness of fit index) according to McAlpine and Eyre (2002) and Spitale et al. (2009). The non-significance of chi-square, a low RMSEA value (0-1), and a high AGFI value (0-1) indicate a better model fit. The model having the lowest RMSEA and the highest AGFI with no significant chi-square value was selected as the best model. We calculated standardized coefficients for each explanatory variable to investigate the relative importance of each.

These analyses were performed using R ver. 3.1.2 (R development core team, 2015). The Bray-Curtis dissimilarity calculations were performed using vegan package ver. 2.3-0 (Oksanen et al., 2015), and SEM was performed using lavaan package ver. 0.5-18 (Rosseel et al., 2015).

3. Results

We collected a total of 15,409 individuals belonging to 63 species (32 species and 5,076 individuals for wetland species and 19 species and 9,481 individuals for open-land species) from all 37 survey sites (Table A1). For wetland species, the values for abundance were smaller in grassland than in other land uses (Fig. 2b) and were similar among newly abandoned farmland, previously abandoned farmland, and wetland sites. For open-land species, estimated richness and abundance were greater in grassland than in wetland sites (Fig. 2cd). Open-land species were also found in newly and previously abandoned farmland sites, though only 1 individual was recorded from the wetland sites (Fig. 2d).

3.1. Species composition in different land uses

The NMDS results showed separate ordination of grassland sites and remnant wetland sites with newly and previously abandoned farmland sites situated between these two land uses (Fig. 3). This pattern of ordination was observed for the two data sets (i.e., wetland and open-land species and wetland species only; Fig. 3). In addition, the composition of wetland species differed among the land uses (Fig. A1). For example, *Trechus (Epaphius) ephippiatus* (*Tre.ep*), *Agonum thoreyi nipponicum* (*Ag.th*), and *Agonum yezoanum* (*Ag.ye*) occurred at both newly and previously abandoned farmland sites, whereas *Loricera pilicornis* (*Lo.pi*), *Bembidion paediscum* (*B.pa*), and *Pterostichus sulcitarsis* (*Pt.sul*) particularly occurred in grassland sites. *Agonum sculptipes* (*Ag.sc*), *Pterostichus nigrita* (*Pt.ni*), and *Chlaenius gebleri* (*Ch.ge*) occurred in remnant wetland sites (Fig. A1); most *Agonum sculptipes* and *Chlaenius gebleri* individuals were also found in remnant wetland (individuals in wetland sites among total individuals; 83.7% and 95.7%). The ANOSIM results showed that species composition did not differ between newly abandoned farmland and previously abandoned farmland or between previously abandoned farmland and remnant wetland ($p > 0.1$, ANOSIM, Table A2) and also showed that the rest of the pairwise combinations of land uses significantly differed from each other ($p < 0.05$, ANOSIM, Table A2).

3.2. Impact of environmental variables on species composition in abandoned farmland

The best fitting SEM showed that soil moisture, amount of wetland area within a 500 m buffer, and abandonment age influenced the dissimilarity index (chi-square = 0.57, RMSEA = 0.00, AGFI = 0.94, Fig. 4b). The dissimilarity index was negatively influenced by soil moisture and the amount of wetland area but was positively influenced by abandonment age (Fig. 4b). Soil moisture was also positively influenced by abandonment age. In the best fitting model, the effects of soil moisture on the dissimilarity index, of wetland area on the dissimilarity index, and of abandonment age on soil moisture were significant ($p < 0.05$; Fig. 4b), with larger effect sizes (Fig. 4b; Fig. A2). The indirect effects on the dissimilarity index, i.e., the effect of abandonment age on soil moisture and the effect of soil moisture on the dissimilarity index, were significant. However, the direct effect of abandonment age on the dissimilarity index was not significant, and the size of the direct effect was smaller than the indirect effect.

4. Discussion

Our NMDS results revealed an apparent difference in species composition between grassland and remnant wetland sites, with the species composition of abandoned farmland being between those of these two land uses. Such an occurrence pattern of wetland species in each land use suggests that wetland ground beetles colonized the grassland after land abandonment and that the composition of wetland species in abandoned farmland is similar to that of remnant wetland. Our results indicated significant effects of abandonment age on soil moisture and of soil moisture on the dissimilarity index. Therefore, the increase in soil moisture over time after abandonment may be one of the main drivers of the changes in species composition in abandoned farmland. Pardo et al. (2008) noted that soil moisture increased after farmland abandonment, and in our study region, increases in time since abandonment resulted in enhanced soil moisture due to age-related malfunctioning of open and underground drainage ditch systems (based on interviews with farmers or local officers). Several studies have reported that wetland species abundance increases with greater soil moisture (Martay et al., 2012; Pardo et al., 2008). In general, wetland ground beetle species can adapt to floodplain environments, such as those with seasonal water level fluctuations (Kolesnikov et al., 2012; Rothenbücher and Schaefer, 2006), and increased soil moisture also contributes to improving habitat quality, resulting in greater egg and larval survival (Huk and Kühne, 1999). Therefore, we conclude that the increase in soil moisture promoted the colonization of abandoned farmland by wetland species. Our results also showed that vegetation density did not affect species composition in abandoned farmland. This could be because vegetation density was similar between newly and previously abandoned farmland sites (Table A3). Previous studies have shown that cultivation legacies such as seed banks and soil nutrients are among the drivers that affect vegetation succession in abandoned farmland (e.g., Bengtsson et al., 2003; Cramer et al., 2008). Although we did not measure seed banks and soil nutrients directly, the fact that vegetation density did not affect the species composition of ground beetles in abandoned farmland (Fig. 4) indicated that the effect of cultivation legacy on ground beetles was limited in this study.

In our study region, wetland area within a 500 m buffer had a significant effect on the dissimilarity index, although the abandonment age and the distance between abandoned farmland and wetland had only a limited effect on the dissimilarity index (Fig. 4b). Overall, the colonization success of meta-communities depends on the dispersal capability of each species and the spatial distance between the source and sink (e.g., Hanski, 2000). Noreika et al. (2015) found that only a few years were required for wetland insects, including ground beetles, to colonize in new restoration sites adjacent to a large and high-quality wetland. The majority of ground beetle species inhabiting unstable habitats have long wings and strong flying capacity (e.g., den Boer, 1990). In fact, more than two-thirds of the wetland species trapped in this study have long hind wings (macropterous species) (Table A1). In addition, Martay et al. (2014) estimated that *Carabus granulatus,* one of the wetland ground beetles, could move up to 2 km in 90 days. In this study area, the distance between the abandoned farmland and wetland was relatively short (tens of meters to several hundred meters on average; Table. A3). Although we could not directly examine their flying ability or movement speed, the wetland species in our study area might be able to move among habitats patches in the agricultural matrix, so they could rapidly colonize abandoned farmland from surrounding wetlands. The amount of source habitat is also an important factor in the colonization of a new habitat by an organism (e.g., Quesnelle et al., 2015) because the dispersal probability (or rate) of individuals to a new patch increases with increasing source patch area. In our study region (i.e., wetland patches located near abandoned farmland), a large surrounding wetland is more important for the colonization of abandoned farmland by wetland ground beetles than other landscape structures.

Our study found that both local and spatial effects (i.e., soil moisture and the amount of surrounding wetland) equally impact the colonization of abandoned farmland by wetland ground beetles, although a direct temporal effect was limited. The results demonstrate that increases in soil moisture and the amount of surrounding wetland can be key for restoring wetland ground beetles using abandoned farmland. Accordingly, we suggest that soil moisture in fields and the surrounding source habitat may be good indicators for understanding whether a given abandoned farmland can serve as a habitat for these wetland species. The cost of restoration of wetland ecosystems tends to be higher than for other ecosystems, such as grassland or woodland (de Groot et al., 2013), and our results showed that abandoned farmland could act as a habitat for wetland ground beetles.

As the reuse of abandoned farmland as arable land in our study region may be difficult due to the large expenditure for repairs to drainage systems, utilizing the natural recovery of wetland vegetation in abandoned farmland may be a cost-effective strategy for restoring wetland environments. For example, rewetting by drainage reclamation (e.g., re-filling drainages with soil) is often used to restore wetland habitat (e.g., Klimkowska et al., 2007), and this technique may be conducted more easily by utilizing abandoned farmland with high soil moisture.

Nonetheless, we should recognize that the natural recovery of wetland species in abandoned farmland does not mean the full restoration of wetland environments. Although the species composition in the examined abandoned farmland sites was similar to that of the remnant wetland, we also found that the species compositions were not equivalent. In fact, open-land species were abundant in the abandoned farmland sites, and some wetland species that were abundant in the wetland sites, such as *Agonum sculptipes* and *Chlaenius gebleri*, were rarely found in the abandoned farmland (Fig. A1). Thus, to efficiently utilize abandoned farmland for habitat restoration, it should be investigated whether the natural recovery of wildlife would fulfill the conservation objectives in the target region and whether additional restorations would be needed. Previous studies have suggested that land improvement, such as rewetting and wetland vegetation transfer, could be efficient methods for restoring wetland species in degraded arable lands (e.g., Klimkowska et al., 2007). When the recovery of wetland specialists is the main conservation objective, such additional management may be an effective strategy for restoring abandoned farmland. In addition, we only examined the colonization success of ground beetles into abandoned farmland in this study, but restoration success also depends on population establishment or persistence in the new habitat (van Andel and Aronson, 2012). Long-term monitoring would be necessary to understand the overall wildlife recovery process on abandoned farmland.

Acknowledgments

We thank the farmers who allowed us to survey on their land as well as three anonymous reviewers for their helpful comments that improved the manuscript. We also thank the members of the Laboratory of Forest Ecosystem Management of Hokkaido University for their assistance with our field survey. This work was supported by a Grant-in-Aid for JSPS Fellows [Number 25-4354]; the Environment Research and Technology Development Fund of the Ministry of the Environment, Japan [Number 4-1504], and a Grant in Aid for Scientific Research from the Ministry of Education, Science and Culture, Japan [Number 15K20842].

References

Barral, M.P., Rey Benayas, J.M.R., Meli, P., Maceira, N.O., 2015. Quantifying the impacts of ecological restoration on biodiversity and ecosystem services in agroecosystems: a global meta-analysis. Agric. Ecosyst. Environ. 202, 223-231.

Benayas, J.M.R., Martins, A., Nicolau, J.M., Schulz, J.J., 2007. Abandonment of agricultural land: an overview of drivers and consequences. CAB Rev. Perspect. Agric. Vet. Sci. Nutr. Nat. Resour. 2, 1-14.

Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F., Nyström, M., 2003. Reserves, resilience and dynamic landscapes. Ambio 32, 389-396.

Boitani, L., Linnell, J.D.C., 2015. Bringing large mammals back: large carnivores in Europe, in: Pereira, H.M., Navarro, L.M. (Eds.), Rewilding European Landscapes. Springer International Publishing, New York, pp. 67-84.

Brambilla, M., Casale, F., Bergero, V., Bogliani, G., Crovetto, G.M., Falco, R., Roati, M., Negri, I., 2010. Glorious past, uncertain present, bad future? Assessing effects

of land-use changes on habitat suitability for a threatened farmland bird species. Biol. Conserv. 143, 2770-2778.
Cramer, V.A., Hobbs, R.J., Standish, R.J., 2008. What's new about old fields? Land abandonment and ecosystem assembly. Trends Ecol. Evol. (Amst.) 23, 104-112.
de Groot, R.S., Blignaut, J., van der Ploeg, S., Aronson, J., Elmqvist, T., Farley, J., 2013. Benefits of investing in ecosystem restoration. Conserv. Biol. 27, 1286-1293.
den Boer, P.J., 1990. Density limits and survival of local populations in 64 carabid species with different powers of dispersal. J. Evol. Biol. 3, 19-48.
Fensham, R.J., Butler, D.W., Fairfax, R.J., Quintin, A.R., Dwyer, J.M., 2016. Passive restoration of subtropical grassland after abandonment of cultivation. J. Appl. Ecol. 53, 274-283.
Fujita, H., Igarashi, Y., Hotes, S., Takada, M., Inoue, T., Kaneko, M., 2009. An inventory of the mires of Hokkaido, Japan—their development, classification, decline, and conservation. Plant Ecol. 200, 9-36.
Gardner, R.C., Barchiesi, S., Beltrame, C., Finlayson, C.M., Galewski, T., Harrison, I., Paganini, M., Perennou, C., Pritchard, D., Rosenqvist, A., Walpole, M., 2015. State of the World's Wetlands and Their Services to People: a Compilation of Recent Analyses, Ramsar Convention Secretariat, Gland, Switzerland.
Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontolol. Electron. 4, 1-9.
Hanski, I., 1999. Metapopulation Ecology. Oxford University Press, New York.
Hanski, I., 2000. Extinction debt and species credit in boreal forests: modelling the consequences of different approaches to biodiversity conservation. Ann. Zool. Fenn. 37, 271-280.
Huk, T., Kühne, B., 1999. Substrate selection by Carabus clatratus (Coleoptera,

Carabidae) and its consequences for offspring development. Oecologia 121, 348-354.

Klimkowska, A., Van Diggelen, R., Bakker, J.P., Grootjans, A.P., 2007. Wet meadow restoration in Western Europe: a quantitative assessment of the effectiveness of several techniques. Biol. Conserv. 140, 318-328.

Koivula, M.J., 2011. Useful model organisms, indicators, or both? Ground beetles (Coleoptera, Carabidae) reflecting environmental conditions. ZooKeys 100, 287-317.

Kolesnikov, F.N., Karamyan, A.N., Hoback, W.W., 2012. Survival of ground beetles (Coleoptera: Carabidae) submerged during floods: field and laboratory studies. Eur. J. Entomol. 109, 71-76.

Kusumoto, Y., Ohkuro, T., Ide, M., 2005. The relationships between the management history and vegetation types of fallow paddy field and abandoned paddy fields (in Japanese). J. Rural Plan. Assoc. 24, 7-12.

MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, Princeton.

Martay, B., Hughes, F., Doberski, J., 2012. A comparison of created and ancient fenland using ground beetles as a measure of conservation value. Insect Conserv. Divers. 5, 251-263.

Martay, B., Robertshaw, T., Doberski, J., Thomas, A., 2014. Does dispersal limit beetle re-colonization of restored fenland? A case study using direct measurements of dispersal and genetic analysis. Restor. Ecol. 22, 590–597.

McAlpine, C.A., Eyre, T.J., 2002. Testing landscape metrics as indicators of habitat loss and fragmentation in continuous eucalypt forests (Queensland, Australia). Landsc. Ecol. 17, 711-728.

Ministry of Environment of Japan, 2004. The national survey on the natural environment (vegetation). http://www.vegetation.biodic.go.jp. (accessed: 16.01.18).

Ministry of the Environment, 2015. Nature restoration project in Kushiro Shitsugen wetland. http://kushiro.env.gr.jp/saisei/ (accessed: 15.02.11).

Morrison, E.B., Lindell, C.A., 2011. Active or passive forest restoration? Assessing restoration alternatives with avian foraging behavior. Restor. Ecol. 19, 170-177.

Navarro, L.M., Pereira, H.M., 2015. Rewilding abandoned landscapes in Europe, in: Pereira, H.M., Navarro, L.M. (Eds.), Rewilding European Landscapes. Springer International Publishing, New York, pp. 3-23.

Noreika, N., Kotiaho, J.S., Penttinen, J., Punttila, P., Vuori, A., Pajunen, T., Autio, O., Loukola, O.J., Kotze, D.J., 2015. Rapid recovery of invertebrate communities after ecological restoration of boreal mires. Restor. Ecol. 23, 566-579.

Oksanen, J., Blanchet, F.G., Roeland, K., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2015. Vegan package. https://cran.r-project.org/web/packages/vegan/index.html (accessed: 16.01.18).

Pardo, M.T., Esteve, M.A., Giménez, A., Martínez-Fernández, J., Carreño, M.F., Serrano, J., Miñano, J., 2008. Assessment of hydrological alterations on wandering beetle assemblages (Coleoptera : Carabidae and Tenebrionidae) in coastal wetlands of arid Mediterranean systems. J. Arid Environ. 72, 1803-1810.

Piqueray, J., Cristofoli, S., Bisteau, E., Palm, R., Mahy, G., 2011. Testing coexistence of extinction debt and colonization credit in fragmented calcareous grasslands with complex historical dynamics. Landscape Ecol 26, 823-836.

Policy Department of Hokkaido Prefecture, 2015. Census for Agriculture and Forestry of Hokkaido.

http://www.pref.hokkaido.lg.jp/ss/tuk/026caf/index.htm?wbc_purpose=Basic (accessed: 16.01.18).

QGIS Development Team, 2015. QGIS geographic information system. http://qgis.osgeo.org/ja/site/ (accessed: 16.01.18).

Quesnelle, P.E., Lindsay, K.E., Fahrigi, L., 2015. Relative effects of landscape-scale wetland amount and landscape matrix quality on wetland vertebrates: a meta-analysis. Ecol. Appl. 25, 812-825.

R Development Core Team, 2015. R: A language and environment for statistical computing. https://www.r-project.org/ (accessed: 16.01.18).

Rainio, J., Niemelä, J., 2003. Ground beetles (Coleoptera : Carabidae) as bioindicators. Biodivers. Conserv. 12, 487-506.

Ramsar Convention Secretariat, 2013. The Ramsar Convention Manual: a Guide to the Convention on Wetlands (Ramsar, Iran, 1971). Ramsar Convention Secretariat, Gland, Switzerland.

Rosseel, Y., Oberski, D., Byrnes, J., Vanbrabant, L., Savalei, V., Merkle, E., Hallquist, M., Rhemtulla, M., Katsikatsou, M., Barendse, M., 2015. Lavaan package. https://cran.r-project.org/web/packages/lavaan/index.html (accessed: 16.01.18).

Rothenbücher, J., Schaefer, M., 2006. Submersion tolerance in floodplain arthropod communities. Basic Appl. Ecol. 7, 398-408.

Sandom, C., Donlan, C.J., Svenning, J.-C., Hansen, D., 2013. Rewilding, in: MacDonald, D.W., Willis, K.J. (Eds.), Key Topics in Conservation Biology 2. John Wiley & Sons, Hoboken, pp. 430-451.

Shoo, L.P., Freebody, K., Kanowski, J., Catterall, C.P., 2016. Slow recovery of tropical old-field rainforest regrowth and the value and limitations of active restoration. Conserv. Biol. 30, 121-132.

Sirami, C., Brotons, L., Burfield, I., Fonderflick, J., Martin, J.-L., 2008. Is land abandonment having an impact on biodiversity? A meta-analytical approach to bird distribution changes in the north-western Mediterranean. Biol. Conserv. 141, 450-459.

Spitale, D., Petraglia, A., Tomaselli, M., 2009. Structural equation modelling detects unexpected differences between bryophyte and vascular plant richness along multiple environmental gradients. J. Biogeogr. 36, 745-755.

Talberth, J., Gray, E., 2012. Global costs of achieving the Aichi biodiversity targets: a scoping assessment of anticipated costs of achieving targets 5, 8 and 14. Proc. Natl Acad. Sci. U.S.A. 105, 9439-9444.

Ueno, S., Kurosawa, Y., Sato, M., 1985. The Coleoptera of Japan in Color, Vol II. Hoikusha, Osaka. (in Japanese)

United Nations, 2016. Population division. http://www.un.org/en/development/desa/population/theme/trends/index.shtml. (accessed: 16.03.02).

van Andel, J., Aronson, J., 2012. Restoration Ecology: the New Frontier. John Wiley & Sons, Malden.

Woodcock, B.A., Redhead, J., Vanbergen, A.J., Hulmes, L., Hulmes, S., Peyton, J., Nowakowski, M., Pywell, R.F., Heard, M.S., 2010. Impact of habitat type and landscape structure on biomass, species richness and functional diversity of ground beetles. Agric. Ecosyst. Environ. 139, 181-186.

Working Group for Biological Indicator Ground Beetles Database Japan, 2015. Natural woodlands ground beetles. http://www.lbm.go.jp/emuseum/zukan/gomimushi/english/index.html. (accessed: 15.04.28).

Zedler, J.B., Kercher, S., 2005. Wetland resources: status, trends, ecosystem services, and restorability. Annu. Rev. Environ. Resour. 30, 39-74.

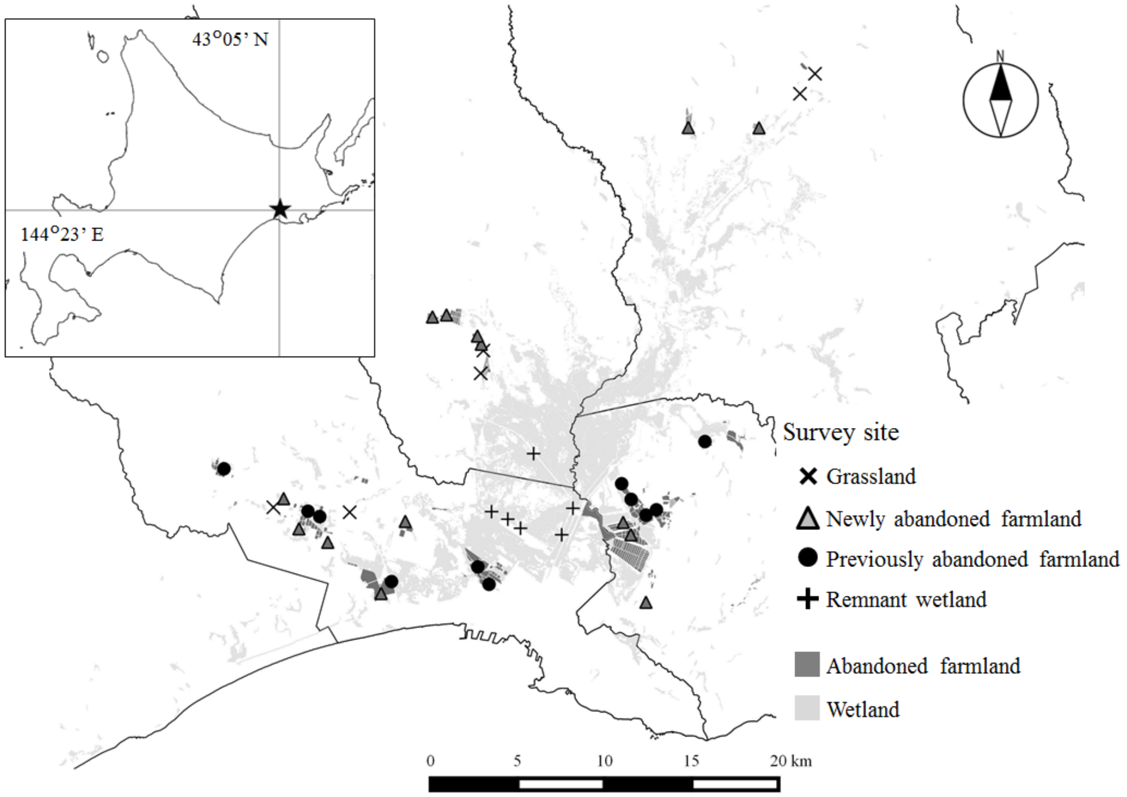

Fig. 1. Locations of the study sites in the Kushiro region, Hokkaido, Japan
Polygons indicate abandoned farmland (dark gray), wetland (light gray), and other land-use types (white). Symbols indicate study sites in grassland (x symbols), newly abandoned farmland (gray triangles), previously abandoned farmland (black circles), and remnant wetland (crosses).

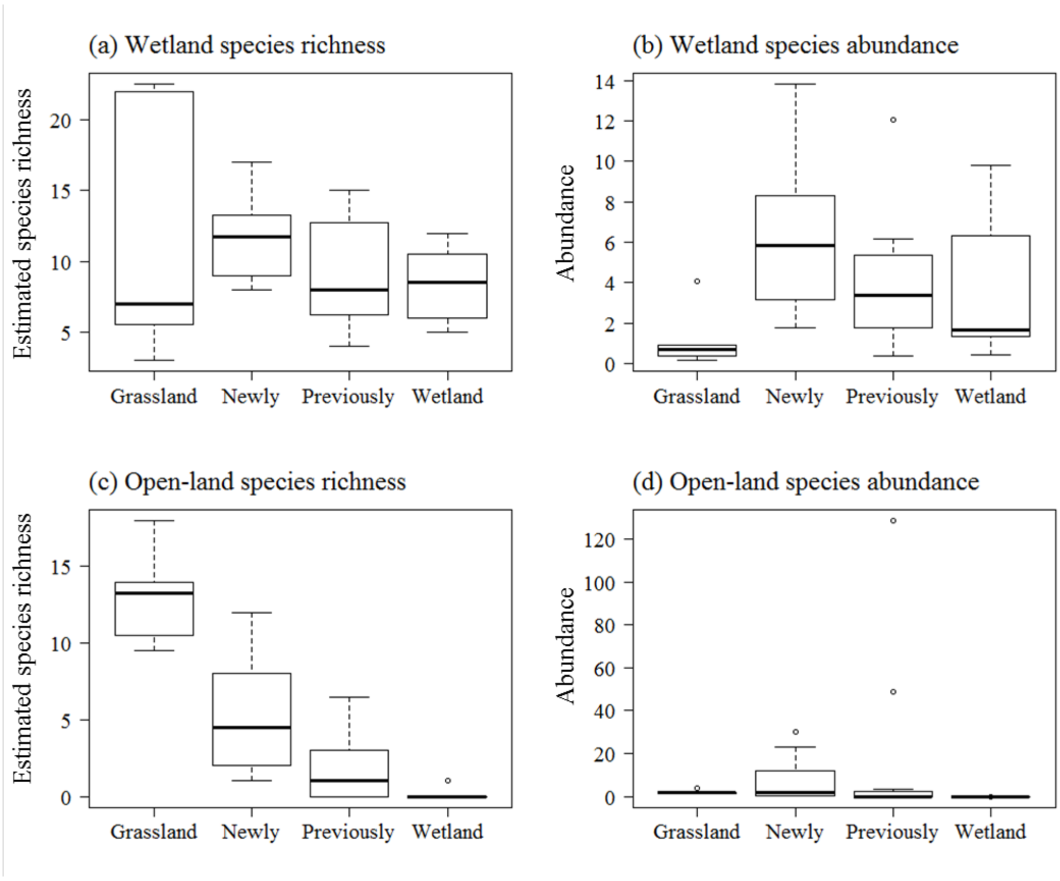

Fig. 2. Boxplot of the richness and abundance of wetland and open-land ground beetle species in four land uses

Wetland and open-land species richness are estimated by the Chao 1 estimator using the vegan package ver. 2.3-0 (Oksanen et al., 2015). Species abundances of wetland and open-land species are presented as the mean values of individuals per trap in each site. The horizontal bars in the boxplot indicate the median, the ends of the boxes indicate the interquartile range (IQR), and the whiskers indicate the lowest data point within 1.5 IQR of the lower quartile and the highest data point within 1.5 IQR of the upper quartile.

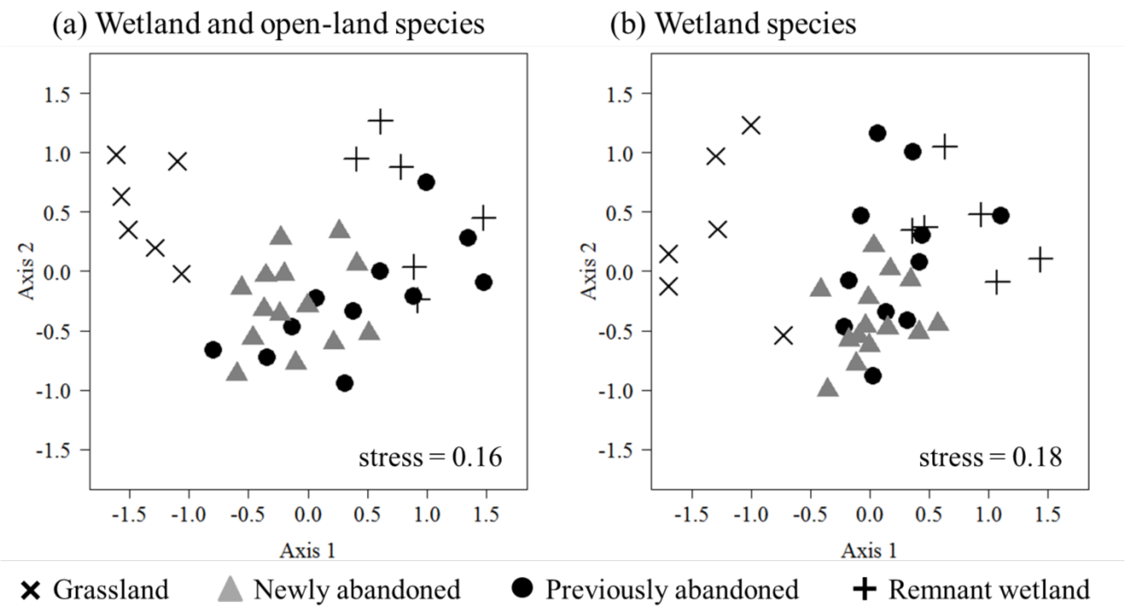

Fig. 3. Non-metric multidimensional scaling (NMDS) ordination of two data sets for each land use: (a) wetland and open-land ground beetle species, (b) wetland ground beetle species

Symbols indicate study sites in grassland (x symbols), newly abandoned farmland (gray triangles), previously abandoned farmland (black circles), and remnant wetland (crosses). The NMDS stress values were 0.16 for wetland and open-land species and 0.18 for wetland species.

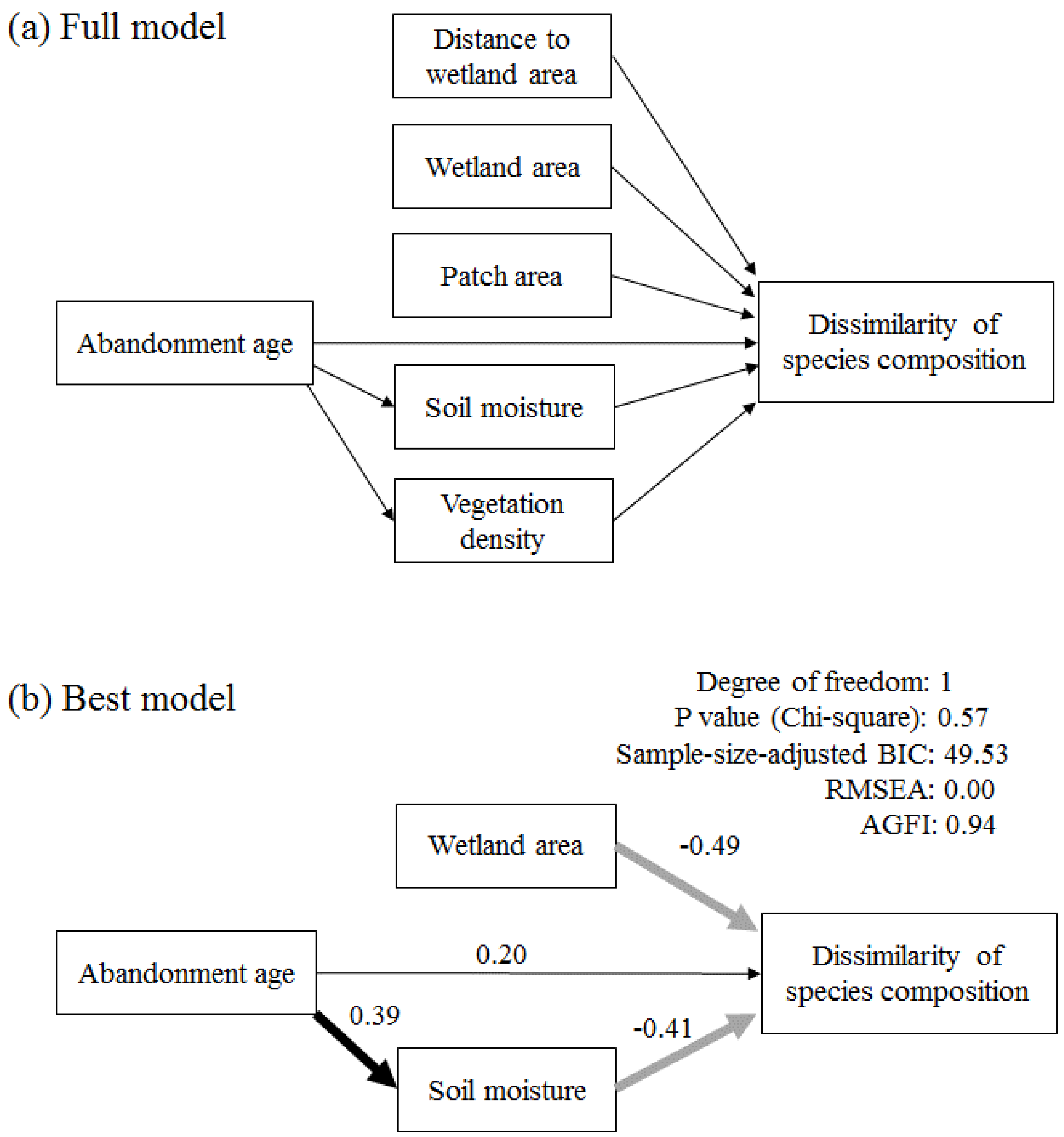

Fig. 4. Results of SEM: (a) full model, (b) best model

The number next to the arrow indicates the parameters of standardized coefficients for each variable. Bold arrows indicate significant parameters ($p < 0.05$). Black and gray arrows indicate positive and negative values, respectively.